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Chapter

Responses of Neotropical Savannah Plant Species to Abiotic Stresses: A Structural and Functional Overview

Silvana Aparecida Barbosa de Castro and Vinícius Coelho Kuster

Abstract

Plants under field conditions are subject to different types of abiotic stresses such as drought, salinity, and light excess that adversely affect their growth and survival. In addition, several studies have pointed out the effect of climate change such as an increase in the concentration of atmospheric CO_2, as well as an increase in global temperature on the distribution and wealth of plants. Adaptation to abiotic stress and survival occurs on different scales, at the cellular level for each individual, and requires a range of strategies, whether morphological, physiological, molecular or structural. Such strategies may be determinant in the distribution of plant species in natural habitats, depending on ecological adaptations shaped by the evolutionary history of species. In this chapter, we discuss recent information about mechanisms of plant adaptation to abiotic stress in the Neotropical savannah based on the cell and individual scales.

Keywords: ecophysiology, water stress, thermotolerance, high luminosity, soil nutrients, fire, Cerrado

1. Introduction

Plants growing under natural conditions are permanently subject to different types of environmental stresses such as drought, nutritional deficiency, salinity, heat stress and, more recently, the anthropogenic pollutants of ecosystems that negatively affect plant growth and survival [1–5]. Moreover, studies have pointed out the effect of climate changes such as the increase of atmospheric CO_2 concentration and global temperature (2 to 4°C) on the distribution and richness of plant species [6–8]. The survival of plant species under such conditions is constantly threatened, leading them to use different cellular and whole plant mechanisms in order to minimize damage and adjust growth to adverse environmental conditions [9, 10]. Plant responses to abiotic conditions have been widely investigated in different ecosystems worldwide, with this issue gaining great prominence for savannas due to the high complexity of abiotic factors that affect the native species of these systems. Among the world's savannas, the Brazilian one, also called Neotropical savannah or Cerrado *sensu lato*, is one of the most diverse in the world in terms of vegetation

and plant species types, recognized as one of the biodiversity hotspots in the world [11, 12]. The Neotropical savannah flora comprises some 12,000 plant species, many of them endemic, two-thirds of which are herbaceous species or small shrubs [13]. The Neotropical savannah covers approximately 22% of the Brazilian territory (**Figure 1**) comprising several physiognomies from open grasslands to woodlands in a mosaic determined by abiotic factors such as edaphic and fire ones [14, 15]. The Campo limpo (grasslands) and Cerradão (tall woodland) are both extreme physiognomies, with great predominance of herbaceous and arboreous strata, respectively [14]. The Campo sujo (shrub savannah), Campo cerrado (wooded savannah), and Cerrado sensu stricto (short woodland) occur between them, with a gradual growth of biomass and larger plant species strata [14]. A mountain physiognomy, called rupestrian fields, also occurs and is restricted to areas of more than 900 m of altitude [16].

The diversity of life-form strategies of the Neotropical savannah plant species is associated with the response to many abiotic factors, especially the climatic seasonality with a well-defined dry and rainy seasons (**Figure 2**). The rainy season normally lasts from October to March, and the dry season from April to September, with an annual rainfall average of about 1,477 mm, a minimum temperature of 16°C and a maximum temperature of 26°C over the past thirty years (**Figure 2**) [17, 18]. High temperatures and irradiance, oligotrophic soils and high content of solubilized Al^{3+} are environmental features of the Neotropical savannah, which select local plant species and induce them to develop physiological and morphological adaptations to this harsh environment [19, 20]. Adaptation to and survival of abiotic stress occur on different scales from the cellular to the individual levels and require a range of strategies, whether morphological, physiological, molecular or structural,

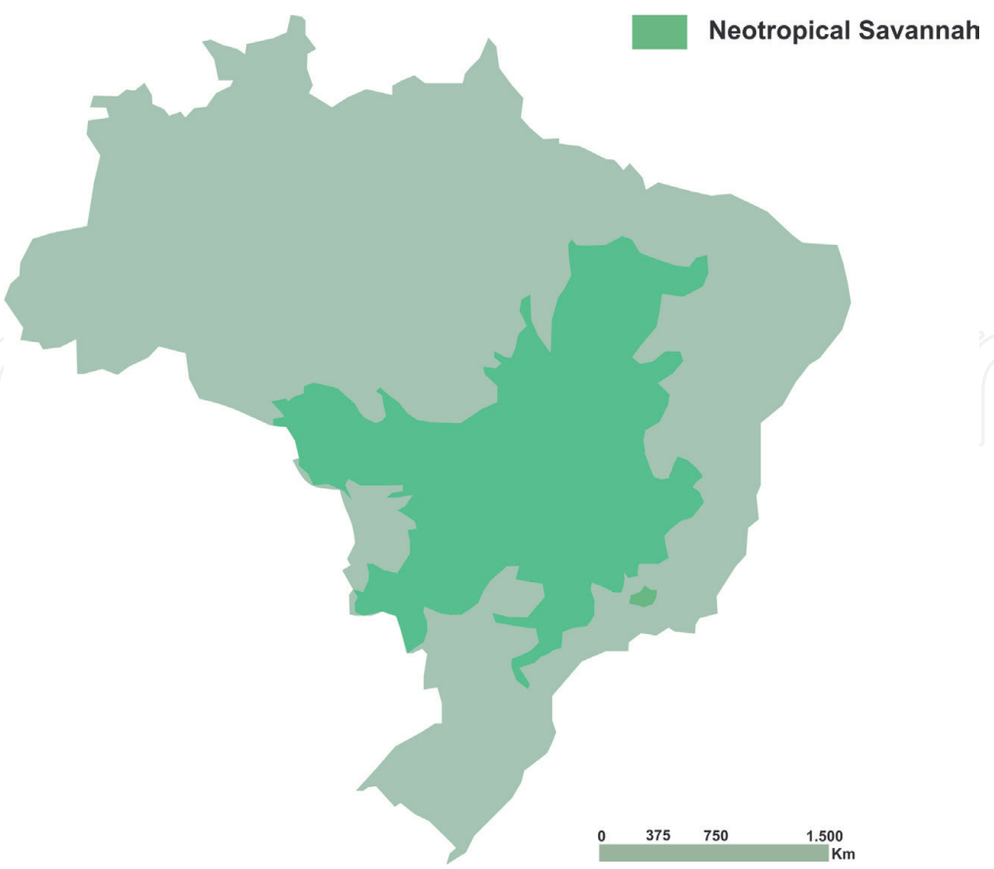

Figure 1.
Map of Brazil showing the occurrence of the Neotropical savannah, which covers approximately 22% of its surface area (Adapted from WWF Brazil, 2020).

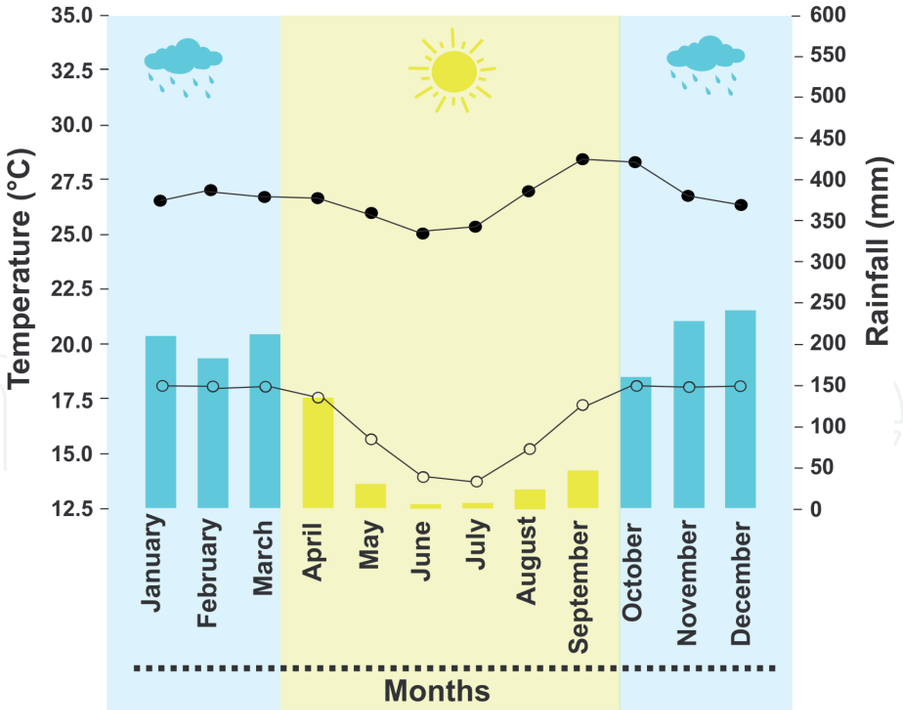

Figure 2.
Rainfall (mm) and temperature (°C) data of the Neotropical savannah during the rainy season (represented in blue area) and the dry season (represented in yellow area), over the past thirty years. Ps.: Black circles indicate the maximum temperature and white circles the minimum temperature (data obtained from Instituto Nacional de Meteorologia - INMET, 2020).

and can be determinant of species distribution in the natural habitats, depending on ecological adaptations shaped by the evolutionary history of the species.

Based on recent studies on Neotropical savannah flora, the focus of this review is on the dynamics and processes related to plant responses to the most prominent abiotic environmental conditions in this ecosystem, mainly highlighting water, temperature, light, nutrient deficiency and fire approaches. We report here information about the different adaptation mechanisms of plant species under the abiotic stress of the Neotropical savannah, from the cell to the individual scales.

2. The water stress seasonality changes the response of plant species during the seasons and along the day

Drought is considered to be one of the major abiotic stresses since it influences the distribution of plant species and limits the productivity of the ecosystems [4]. All aspects of plant development, i.e. germination, cell division, cell elongation, plant growth, and metabolic activities, are affected by a reduction in soil water content, which subsequently affects the physiological, biochemical, morphological and molecular processes of plants [21, 22]. Water flow from the soil to the roots depends of several factors, such as, potential water gradient between the soil and the plant, the hydraulic conductivity of the soil, the soil moisture content, and the atmospheric demand, that together with leaf transpiration create a tension in the xylem contributing to the creation of this water potential gradient [22, 23].

Regarding water stress, physiological and biochemical responses are more immediate in order to avoid cell dehydration, to maximize the efficiency of water use or to tolerate dehydration [1, 24]. The ability to maintain higher values of cellular water content is known as a strategy of plants sensitive to drought conditions. On the other hand, the ability to survive with lower values of cellular water content

is called drought tolerance and requires the expression of molecular mechanisms since the initial growth of the seedling [25, 26]. Drought-tolerant plant species can be found in ecological niches with water seasonality, especially in the Neotropical savannah [27]. Drought-sensitive plant species also occur at the same sites as those of drought-tolerant ones; however, they use different molecular, biochemical, and physiological mechanisms to prevent desiccation, and thus deal with the lack of water in the soil. Drought-tolerant plants are able to limit damage to a repairable level in order to maintain physiological integrity due to the occurrence of repair mechanisms triggered by the dehydration/rehydration cycle [27, 28]. During long periods of drought, maintaining cell homeostasis and withstanding dehydration seems impractical for plants, directly impacting their growth rates [4, 27].

The Neotropical savannah abiotic conditions such as high irradiance, elevated air temperature, and low relative humidity impose a high evaporative demand on plants during the dry season while at the same time water is exhausted in the upper layers of the soil [29, 30]. Water use by Neotropical savannah woody plants is limited by a combination of physiological, plant architectural and tree density constraints evidencing that water use by the plant community seems to be more complex than in other savannas [30]. Even in the dry season, the water supply remains constant in the deeper soil layers, allowing access to water for tree species with long roots (in trees and shrubs) and differences between functional groups may be more related to the topography of an environmental continuum in which grass species are most subject to water restriction (**Figure 3**) [30, 31]. The hydrological niche segregation, defined as a fine scale partitioning of space for soil moisture gradients or different strategies of water acquisition, has been pointed out in different plant communities [32, 33] including the Neotropical savannah physiognomy [34, 35]. A marked decrease in water potential during the dry season has been reported for several species of the Neotropical savannah both in predawn and midday measurements [31, 35–37]. However, the water potential can vary according to the microhabitat, with plant species in mesic microhabitats showing smaller drops in the values of water potential even during the dry season (**Figure 3**). Costa et al. [38] also observed a decrease in water potential in *Hymenaea stigonocarpa* (Fabaceae) subjected to water stress, followed by recovery after rehydration. In an experimental study with *Laivosiera campos-portoana* (Melastomataceae), França et al. [39] reported that drought stress triggered a decrease of stomatal conductance and that osmotic adjustment played an important role in keeping high relative water content (RWC) values. These data suggest that the maintenance of high RWC values in plant species, despite a decrease in xylem water potential during the dry season, may be related to adjustment to stress, allowing survival in different microhabitats.

Plant responses to water deficit occur in different forms and scales, e.g. morphological, physiological, biochemical, and molecular ones, which may occur at the same time or at different times. For instance, the synthesis of cellulose microfibrils, hemicelluloses, and pectins in the cell wall may be changed under water stress, especially regarding the cell elongation pattern [40–42]. Strategies for adaptation and survival under water deficit conditions are also associated with the production and accumulation of organic solutes such as glycine-betaine, proline, and soluble sugars, which protect the integrity of the membrane and promote osmotic adjustment [43–47]. In addition, an increased content of several amino acids such as glutamic acid, glutamine, lysine, proline, serine, tryptophan, tyrosine and valine has been reported after water stress imposition in Neotropical savannah species [47, 48]. Proline is an important osmoregulator that protects plants submitted to abiotic stresses, favoring osmotic adjustment and an increase in the other osmolytes [20]. Souza et al. [48] detected increased carbohydrate content in *Hymenae courbaril* (Fabaceae) roots subjected to water deficit, which appeared to be directly linked to

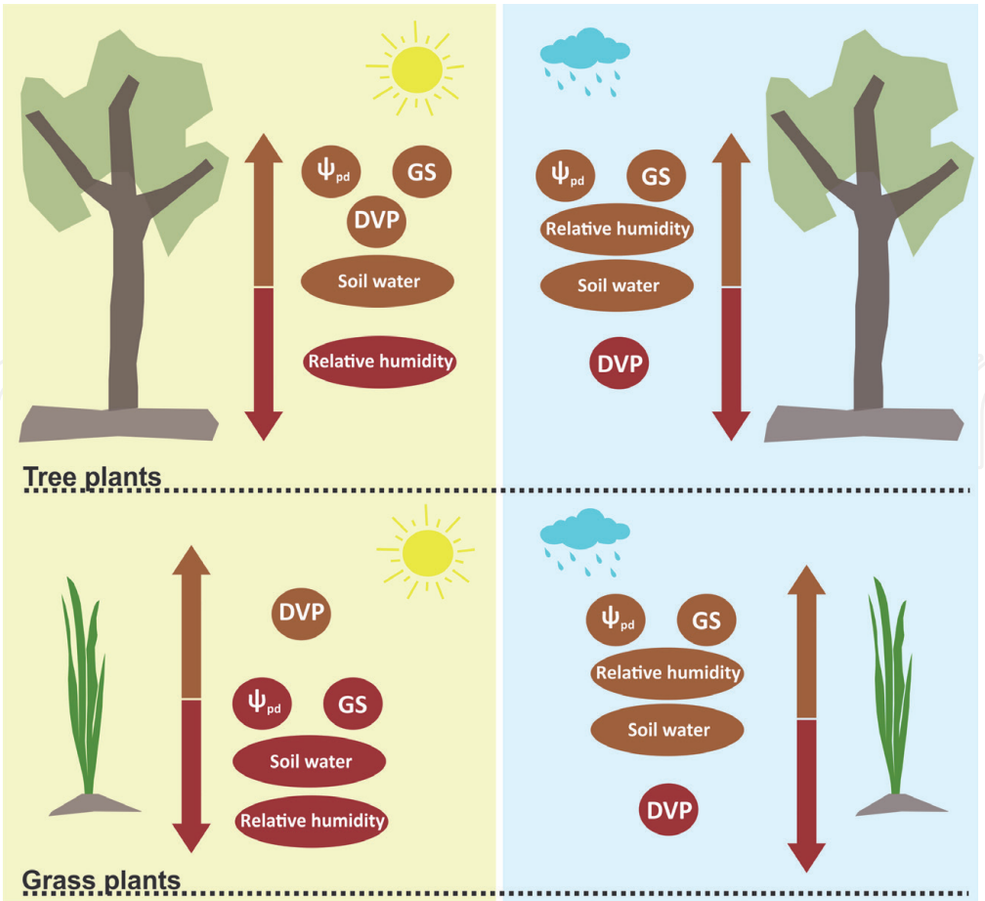

Figure 3.
Schematic presentation of the main physiological responses of tree and grass species from the Neotropical savannah in terms of water availability during the rainy (represented in blue area) and the dry season (represented in yellow area) seasons. Brown arrows indicate an increase in rates while the red arrows show a decrease. Abbreviations: *ψpd- predawn leaf water potential; GS- stomatal conductance; VPD- relative vapor pressure deficit.*

the osmotic adjustment of the cell. Some studies have indicated an accumulation of sucrose, raffinose and arabinose during the dry season, while glucose and fructose levels decreased with the reduction of water availability in the soil, suggesting that these are used for sucrose synthesis [49, 50].

The plant antioxidant system also plays a key role in water stress by responding with the production of enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione peroxidase (GPX), as well as non-enzymatic components such as ascorbate, glutathione, tocopherols (vitamin E) and carotenoid pigments [51, 52]. Imbalance in the production of reactive oxygen species (ROS) has been demonstrated to affect negatively cell membrane stability, with oxidative damage to carbohydrates, lipids, amino acids, proteins, and nucleic acids [51]. ROS play a key role in the process of plant acclimation to abiotic stress such as signal transduction, which regulates different pathways during plant acclimation to stress [53]. Moreover, many plants may rapidly produce and scavenge different forms of ROS, inducing fast and dynamic changes in ROS level [51]. Under normal growth conditions, ROS are continuously produced and scavenged in organelles such as chloroplasts, mitochondria, peroxisomes and apoplasts [54]. However, the balance between ROS-producing pathways and ROS-scavenging mechanisms may be disrupted when plants experience environmental stress such as drought [52, 55, 56].

Regarding the photosynthetic apparatus, Assaha et al. [57] reported a super excitation of photosynthetic pigments after ROS accumulation in plants under

severe water deficit. For instance, increase in oxidative stress (i.e. increase of H_2O_2) and in SOD, CAT, and APX activity in roots was reported in two Neotropical savannah tree species subjected to water stress imposed by competitive species [58]. As well, Vieira et al. [58] also showed an increase in the activity of enzymes of the antioxidant system in *Vatairea macrocarpa* (Fabaceae) subjected to water stress. Besides, ROS detoxification systems, other strategies are essential for plant tolerance to drought, such as a reduction in chlorophyll synthesis and in the assimilatory apparatus components, as well as a balanced sugar pentose-phosphate pathway [59–61].

The seasonality of water availability can also result in dynamic photoinhibition in woody plants [62], but not in herbaceous species [63–65]. A reduction of stomatal conductance and of net CO_2 assimilation has also been reported in *Barbacenia Purpurea* (Velloziaceae) submitted to water stress, but recovery was detected hours after rehydration [50]. Decreased stomatal conductance followed by a reduction in photosynthetic rates in plants under moderate water deficit has been reported [66]. Midday depression is related to excessive sunlight exposure and has been shown for a wide range of plant species of the Neotropical savannah, with impact on photosynthesis and on CO_2 assimilation [62, 67, 68]. The reduction of the Fv/Fm ratio, of maximum variable fluorescence (Fv) and of maximum fluorescence (Fm) during the dry season seems to be a consequence of a combination of strong stomatal control, especially in shrub species, high irradiance, and low soil moisture conditions [35, 67]. Stomatal control may prevent the dissipation of excessive energy and lead to chronic photoinhibition in some Neotropical savannah plant species [68]. Chronic seasonal photoinhibition has been shown for some plant species in the xeric microhabitat of the Neotropical savannah, as reported for Melastomataceae species, although it does not occur in mesic habitats [35, 63, 69]. These data reveal the importance of the specific characteristics of the microhabitat in the physiological studies of plants despite the seasonal variation of water availability. Several factors such as microhabitat, root system, functional group and topography directly influence water use strategies by the plant community, causing the Neotropical savannah to be more complex than other savannas.

3. Thermal stress triggers morphological and physiological damage and acts as selecting factor

Plants have different temperature domains that initially determine their geographic distribution [70] but with the progressive increase in air temperature, the temperature domains become displaced to colder regions, forcing plant species to move away from their current distribution [71, 72]. The increase in temperature may cause several types of damage to plants in different stages of life, from germination to adulthood [73, 74]. The temperature range considered optimal for photosynthesis in C3 plants is between 18°C and 30°C, while temperatures above 30°C are considered to be heating zones [70, 75]. Thermotolerance acquisition occurs when a plant is exposed to low or high temperatures for a short period of time, up to a limit where no fatal injuries occur [8] being thermotolerance fundamental for the plant to deal with greater variation in temperature under certain conditions.

Morphological damage has been reported for vascular plants as a response to heat stress, with emphasis on leaf and branch burn, foliar senescence and abscission, inhibition of shoot and root growth, discoloration, and fruit damage [76]. Associated with the damage triggered by heat stress, the response to rising temperatures varies widely among plant species, functional groups and life strategies [77, 78]. For instance, fast-growing plants from tropical forests in high

light environments tend to be more tolerant of high temperatures than slow-growing plant species typical of shaded places in the understory [77]. According to Franco et al. [79], there is controversy over the limiting processes that control photosynthesis at high temperatures, with different responses in the metabolism of C3 and C4 plants. In particular, under high temperatures, the photosynthetic rate (A) can increase up to a point above which it starts to be inhibited and can reach zero [77]. At higher temperatures, plants show elevated stomatal conductance as a way to dissipate excess heat on leaf surfaces. However, in combination with water stress, greater control of stomatal opening can limit heat dissipation with an impact on photosynthesis [60, 80, 81]. The reduction of photosynthesis occurs due to damage to the electron transport chain associated with increased fluidity of the thylakoid membrane and damage to photosystem II (PSII) [82, 83]. PSII is highly sensitive to temperature and damage can be observed after a few minutes to a few hours of exposure to heat [60, 84, 82, 85]. A reduction in the membrane lipid content and an increase in lipid degradation during the late period of stress with formation of ROS exposure has been reported and the balance between ROS production and elimination is rapidly disturbed, leading to an increase in ROS content [86]. Changes in chlorophyll content in plants exposed to high temperatures have also been reported, possibly due to inhibition of chlorophyll biosynthesis for the destruction of numerous enzymes involved in their biosynthesis [87].

A highly consolidated mechanism of heat acclimation and rapid response to high temperature in plants is the production of heat shock proteins (HSPs), which are key for thermotolerance acquisition [88]. HSPs protect intracellular proteins from denaturation and preserve their stability, thus acting as chaperones [88–90]. According to Ohama et al. [90], HSPs include HSP100, HSP90, HSP70, HSP60 and small HSPs that play a key role in protein quality regulation by renaturing a variety of proteins denatured by heat stress. Together, HSPs and ROS scavenging enzymes are the major functional proteins induced by heat stress [90].

Duarte et al. [91] detected increased oxidative stress at high temperatures in seedlings of the Neotropical savannah plant species *Vriesea friburgensis* and *Alcantarea imperialis* (Bromeliaceae) due to the accumulation of H_2O_2, which in turn led to a decrease in the number of leaves and in biomass and to a high mortality rate in *Vriesea friburgensis* when submitted to treatment at 35°C. Under field conditions, Neotropical savannah plant species show photoinhibition during the hottest hours of the day, especially in combination with seasonal water stress [62, 92]. Changes in morphological traits have been observed for other Neotropical savannah plant species, such as germination in *Dipteryx alata* (Fabaceae) in an experiment involving increasing temperatures [93] and in the response to zinc absorption in *Pterogyne nitens* (Fabaceae) [94]. Changes more directly related to photosynthesis, water use efficiency, growth rate, factors that can alter the competitive capacity of species, have been observed [73, 95, 96].

Model-based studies predict changes in plant species distribution and loss in areas with greater biodiversity due to increased worldwide global temperature [97–100], also affecting the Neotropical savannah [100, 101]. Chaves et al. [102], in a study of a restricted plant species from the rupestrian field, showed that although some plants were no longer sensitive to the increase in temperature, they showed lower thermal tolerance and less plasticity compared to plant species of wide distribution, with a possible impact of global climate changes on this species. A recent modeling study evaluating the effect of habitat loss and climate change on 2,354 species of restricted distribution (including the Neotropical savannah) showed that 70 to 85% of them are at high risk of extinction [103]. With the increase in global temperature it is possible that plant species may be following three paths: adapting through phenotypic plasticity, migrating to higher altitude, or

becoming extinct [7, 101]. Bueno et al. [104] showed that the greatest expansion of the Neotropical savannah occurred precisely during periods of higher temperatures (Last Interglacial). However, this result was certainly based on climate stability that allowed a large number of plant species to persist over time to the detriment of areas with major climatic changes where species might not have had enough time to adapt or to move to regions with more favorable conditions [105, 106].

Multiple environmental factors vary with increasing altitude, with temperature being perhaps the most important one because it directly influences biochemical processes related to photosynthesis and water status. Therefore, studies that evaluate the physiological responses of plant species at high temperatures are important because they provide data that can generate models of future plant species distribution considering different scenarios of temperature change, and because they serve as the basis for public policies aimed at protecting areas with plant species most vulnerable to global climate change.

4. Neotropical savannah plant species must deal with spatial and temporal light heterogeneity

Light is one of the abiotic factors that influence the survival, development and growth of plants, and several traits are highly plastic in the presence of substantial variations in the amount of light received, especially traits related to light capture and photosynthesis [107–110]. Light also shows spatial and temporal heterogeneity as an important factor underlying niche partitioning among plants [111, 112], which has created plants adapted to a variety of light intensity, such as sun-adapted and shade-tolerant plant species [113]. For photosynthesis, the flux of photons in the 400–700 nm range is the most relevant variable to be considered in studies that evaluate changes in light intensity on the development and growth of plants [110]. Under high-light conditions, plants possess a variety of mechanisms that maintain the operational photosynthetic system, such as carotenoids, violaxanthin, antheraxanthin and zeaxanthin, which play an important role in the dissipation of excitation energy at times when light levels exceed the plant capacity for photosynthetic electron transport and carbon fixation [114, 115]. However, plants exposed to high radiation may suffer increased leaf temperature, resulting in photoinhibition of Photosystem II (PSII) [116, 117].

In tropical regions, the irradiance levels normally exceed those that plants use in photosynthesis, so that many plants have efficient mechanisms preventing or minimizing the damage to the photosynthetic apparatus caused by high light availability [118]. Nevertheless, different light regimes in each physiognomy can promote the establishment of different plant species or functional traits [119]. Regarding the Neotropical savannah, most plant species are well adapted to high light intensity, and at the same time they may have low plasticity for adaptation to and growth in shaded environments [120, 121]. Under contrasting light conditions, some traits such as stomatal conductance, chlorophyll and carotenoid contents have been shown to have higher rates of plasticity in plant species growth and in different seasons (i.e. dry and rainy seasons) [120, 122]. According to Franco et al. [92], a balance between the use of light absorbed for photosynthesis and the dissipation of potentially harmful excess light is essential for Neotropical savannah plant species since they still have to deal with other abiotic factors (i.e., high air temperature, low relative humidity and seasonal drought). Regarding the photosynthesis apparatus, Franco et al. [92] also reported that woody plant species are capable of maintaining the functionality of PSII under conditions of high irradiance and high evaporative demand of the atmosphere during long sunny periods

at the end of the dry season. In contrast, in a study of *Hymenaea stigonocarpa* (Fabaceae) under high light intensity, Fv/Fm values decreased to 0.64, indicating the occurrence of photoinhibition as well as a lower water potential value [123]. In a study of *Copaiba langsdorffii* (Fabaceae) growing under full sun and shade conditions, Ronquim et al. [119] observed that juvenile plants under full sun conditions showed higher maximum net photosynthetic rates, light compensation and saturation points than juvenile plants growing under shade conditions. Other leaf traits associated with light have been pointed out, such as low specific leaf area (SLA) values and high carotenoid and chlorophyll content in plant species from open areas, which may represent adaptive mechanisms to high luminosity environments [36, 79, 121].

In another approach, recent studies have considered the impact of plant invasions in open areas of the Neotropical savannah caused by the widespread expansion of forest in the absence of fire, which tend to change the availability of light for native species already adapted to high radiation [121]. In areas with invasion and expansion of forest, changes in leaf area index (LAI) have been reported, as well as changes in the photosynthetically active radiation available to Neotropical savannah plant species [124]. Moreover, Rossatto et al. [121] showed that invasion of originally open savannah areas by forest trees has an impact on the persistence of savannah plant species, which need greater availability of light to maintain a positive carbon balance. Under these conditions, it is expected that grasses and herbaceous species, already adapted to high light availability, will not be able to maintain the CO_2 assimilation necessary for the maintenance of root carbon stock, which is essential for adaptation to fire and seasonal water stress.

5. Neotropical savannah plants live in nutrient-poor soils with aluminum phytotoxicity

The Neotropical savannah soils are considered to be among the most chemically infertile soils in the world [124, 125], being generally dystrophic, acidic and poor in available nutrients [126, 127], as well as having high levels of exchangeable aluminum (Al) [127, 128]. Soils are mainly represented by well-drained oxisols [129], named "latossolos" in the Brazilian soil classification system [130], followed by sandy entisol, ultisol and cambisol soil types [129, 131]. Many relevant plant nutrients such as K, Ca, Mg, N, S, and P, are deficient in the soil of most Neotropical savannah physiognomies due to the nutritional deficiency of the initial matrix rocks and the intense weathering that leads to daily loss of nutrients [127]. Although Neotropical savannah soils are generally defined as dystrophic, mesotrophic physiognomies have also been reported [132, 133], influencing the variation of floristic structure, as reported by Neri et al. [133] when differentiating dystrophic and mesotrophic Cerradão physiognomies.

In the nutritional approach to studies of the Neotropical savannah, aluminum phytotoxicity and the responses of native plants to low nutrient availability, mainly nitrogen and phosphorus, are some of the most highlighted topics, which will be discussed here. Al is one of the main metals present in the crust of the Earth [134], being a limiting factor of plant development [135, 136]. Most Al is available in soils in the form of non-phytotoxic elements such as Al oxides and Al silicates [137]. However, under acid conditions (pH < 5), Al is solubilized to Al^{3+} [138–140], as well as to $Al(OH)^{2+}$, $Al(OH)^{2+}$ and $Al(OH)_6{}^{3+}$ [141], all known as phytotoxic forms. The relationship between Al phytotoxicity and acidic soils stands out mainly in the Neotropical savannah, where some physiognomies such as Neotropical savannah *sensu stricto* and associated open physiognomies contain acid soils [126]. High Al

concentrations, especially Al^{3+}, occur in dystrophic soils, while soils almost free of exchangeable Al occur in mesotrophic physiognomies with pH > 6.0 [127, 133, 142].

Al^{3+} is extremely toxic for the majority of cultivated plants, but, as expected, the native Neotropical savannah plants are highly tolerant to it [133] and may be divided into Al-accumulating and non-accumulating plants [143–145]. Plants that store 1000 mg kg^{-1} Al are defined as Al-accumulating species [127, 144, 146], which can accumulate Al in roots or aerial parts [142]. For instance, *Qualea grandiflora* (Vochysiaceae), *Qualea cordata* (Vochysiaceae) and *Miconia albicans* (Melastomataceae) have been reported to be Al-accumulating species [132, 147]. Moreover, concentrations of about 20,000 mg Al kg^{-1} dry leaves have been observed for some native Al-accumulating plant species of the Neotropical savannah [132, 143] such as noted for *Vochysia tucanorum* (Vochysiaceae) [132]. Many Al-accumulating plant species not only tolerate Al but also need it for their growth and development, as is the case for some plants of the Rubiaceae, Melastomataceae, and Vochysiaceae families [148]. Thus, Al-accumulating plant species, in many cases, reduce their growth rates when subjected to the absence or a low concentration of aluminum [127, 147, 149]. On the other hand, many plant species do not accumulate more than 1000 mg/kg^{-1} Al in their leaves, as reported for 24 out of 32 plants from the central part of the Neotropical savannah, such as *Caryocar brasiliense* (Caryocaraceae), *Vellozia squamata* (Velloziaceae) and *Roupala montana* (Proteaceae) [143].

Reduced developmental rates and physiological changes may be some symptoms related to high Al concentrations in non-Al accumulating Neotropical savannah plants. The inhibition of root growth [103], the lack of lateral roots [150], and a low biomass of stems and leaves [141, 148, 151] have been demonstrated in plants growing in the presence of high Al concentrations. According to Čiamporová [152], the inhibition of root growth may be due to Al impregnation of root cell walls that promotes unequal expansion and changes in tissue organization. This process occurs in many Al-sensitive plants, while in Al-tolerant species the high Al deposition on the cell wall normally does not inhibit root elongation, as reported for soybean seedlings [153]. Organic acid exudation from the roots has been cited as an important strategy for Al exclusion [150, 154], which avoids Al uptake and the associated structural and physiological symptoms. Bittencourt et al. [155] have shown that *Styrax camporum* (Styracaceae) releases organic acids in the roots as a defense mechanism against high Al accumulation. However, this process only works when the plant is exposed to low to moderate Al levels.

Regarding the physiological responses, previous studies have demonstrated that CO_2 assimilation rate and stomatal conductance were reduced in Al non-accumulating species submitted to high Al concentrations [150, 151, 156]. The leaf gas exchange performance of Al-sensitive species has been associated with the lack of lateral roots [150, 157, 158], which are the plant's water uptake site. The lack of a water supply from the roots reduces its amount in the mesophyll, leading to low gas exchange [159]. Associated with reduced gas exchange performance, the CO_2 assimilation rate was also reduced in some plant species submitted to high Al doses [160], as reported for *Citrus* [161, 162] and for two sorghum cultivars [163]. From a photochemical perspective, quantum yield, maximum variable fluorescence ratio (Fv), minimum fluorescence (F_o), and Fv/Fm have been reduced in the presence of high rates of Al [164], an event that seems to be related to the impairment of PSII photochemistry [163] to the reduction of PSII electron transport [165], and to other changes in photochemical processes. However, substantial changes in Fv/Fm values have not been observed in Al accumulating and Al non-accumulating species subjected to high Al concentrations [147, 150].

In contrast to Al, nitrogen (N) and phosphorus (P) are reported as the limiting factors in the Neotropical savannah [166] both due to the old age of the soil and to the recurring effect of fire, which contributes to the volatility of N parts [167, 168]. N is a prevalent element in living systems and is a constituent of phytohormones, amino acids, proteins, nucleic acids, and enzymes [169]. It acts on the initial growth processes, helping with the synthesis of deoxyribonucleic acids and the replication of chromosomes [169]. P is also required for plant development since it is involved in metabolic regulation, such as amino acid synthesis and protein activation [170], and is also a constituent of ATP/ADP and phospholipids [171]. Thus, N and P are nutrients required in large amounts for initial plant development [172]. According to Reis et al. [173], both nutrients are normally present in limited amounts in Neotropical savannah soils since low N availability may be related to the presence of minimal organic matter and to the fact that P is low in soils containing iron and aluminum oxides [174], both typical conditions of most Neotropical savannah soils. N and P are constituents of photosynthetic process-related proteins such as plant pigments [141], thus representing fundamental elements for the maintenance of photosynthetic quantum yield and biochemical steps. For instance, *Eugenia dysenterica* (Myrtaceae) seedlings showed increased photosynthetic activity and growth with N fertilization at rates between 50 and 200 mg dm^{-3}, while P fertilization at rates of 100 mg dm^{-3} and 200 mg dm^{-3} increased growth and photosynthetic activity, respectively [173]. In addition, some findings suggest that the growth of many plant species is reduced in Savannah soils, although the chemical attributes *per se* do not seem to exclude the occurrence of plants in Neotropical savannah physiognomies [175]. Despite the low availability of N and P, plant species growing in Neotropical savannah soils have a variety of mechanisms dealing with shortages of these nutrients. For instance, P is allocated to photosynthetically active mesophyll cells, showing higher photosynthetic P-use efficiency (PPUE), association with mycorrhizal species, different ways of nutrient uptake, and an efficient use of nitrogen [168, 176].

From another perspective, over the last decades, the Neotropical savannah has suffered enormous losses of its original cover (more than 50%) [11, 177]. Moreover, the change in land use, such as the introduction of extensive pecuary and immense extension of soybean crops, has contributed to the growing supply of these nutrients in the Neotropical savannah soils [178]. Studies have shown that the increase in N and P favors the increase in biomass, the decrease in species richness, the establishment of invasive species and changes in plant structure (root/shoot ratio, and root structure) and in competitive relationships [179–181]. It has also been shown that ancient ecosystems with less P availability in the soil are the richest in plant species [182, 183]. Thus, it is expected that an increase in P supply in the Neotropical savannah soils may have an impact on plant species richness in the medium and long-term.

6. Fire as a selective agent for plant communities

Fire has shaped different terrestrial environments since early geological ages and has been part of Earth's system since the origin of land plants in the Silurian period [184, 185]. In the Neotropical savannah, fire is one of the determining factors that select and structure plant communities and that promote the cycling of nutrients, representing a fundamental abiotic agent for the maintenance of open ecosystems [186, 187]. In the phytophysiognomies of the Neotropical savannah, fire normally occurs at the end of the dry season [188] as a result of the highly combustible

material of dry herbaceous plant organs (**Figure 4**), while during the rainy season, natural fires can be caused by lightning [187, 189]. Although fire is a natural and periodic component of this environment, anthropic activities have intensified its action and made it more frequent [190], leading to cyclic burning of the herbaceous layer and a marked reduction of the maintenance and renewal of trees and shrubs, progressively decreasing their density [191]. Thus, the main problem with fire is that it is seen as a bad event when its regime (frequency, extension, and intensity) is somehow changed [187, 192].

Given the seasonality of fire in the Neotropical savannah, plants possess physiological, morphological, ecological, chemical, and phenological adaptations to deal with it. These adaptations, as well as adaptation to drought (*see* [193]), can enable plant species to escape from fire, as is the case for plants with a short life cycle, or to resist fire, as is the case for tree species with extra protective bark [194]. As an escape strategy, many herbaceous species synchronize seed production before annual burning periods and enter a type of dormancy that only ends after high-temperature exposure [192], as reported for different plant species. For instance, the dormancy of *Sporobolus cubensis* (Poaceae), a herbaceous species of the Neotropical savannah, was broken by exposure to 200°C, indicating the need of fire temperature for its germination [195]. However, many seeds and underground plant organs may be protected against scorching since the heat from fire events does not reach deeper layers of the soil [196]. In general, a fire event is followed by a high germination rate and seedling development since the supply of nutrients increases from the ashes and more light reaches the plant from the opening of canopies [192, 197].

In a phenological approach, fire can affect vegetative and reproductive phenophases [186], leading to leaf abscission by the heat created from the fire, as well as decreasing the numbers of flowers and fruits [191, 198]. However, Silvério et al. [199] reported that the negative effects of fire on the vegetative phenophases were normally followed by an increase in sprouting and the production of leaves, revealing an epigeous recovery mechanism from fire damage. In a reproductive approach, Pilon et al. [200] reported a similar pattern, with fire triggering the production of flowers and fruits in 79% of 47 plant species such as grasses, forbs, and subshrubs. Moreover, several studies have reported flowering in several plant species after the passage of fire [201, 202] and, more recently, Fidelis et al. [203] reported massive

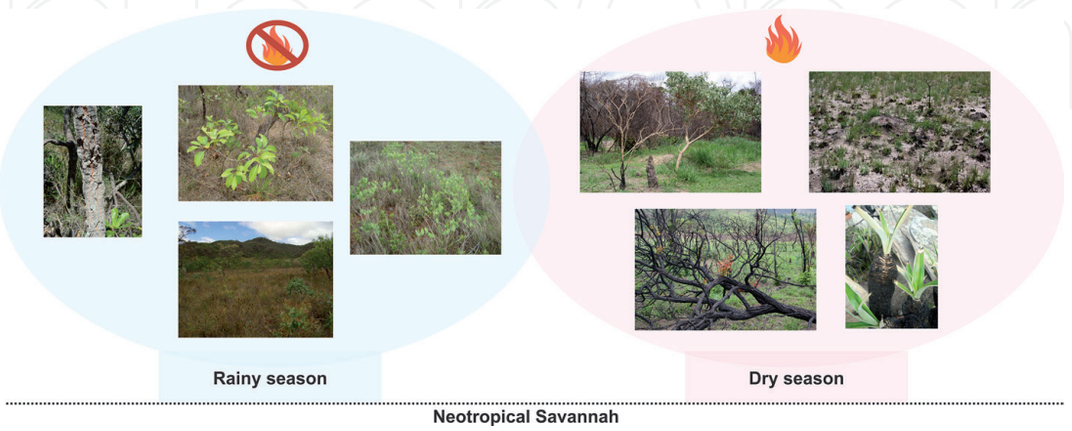

Figure 4.
Overview of the Neotropical savannah plant species in the pre-fire (blue circle) and post-fire (pink circle) periods, which coincided with the rainy and dry seasons, respectively. At a pre-fire time during the rainy season, the herbaceous stratum exhibits dry and flammable aerial organs, while tree and shrub species have green and photosynthesizes leaves. At a post-fire time during the dry season, the leaves of the herbaceous stratum regrow, while many tree species are still leafless due to leaf loss caused by heat, and with a stem blackened by the action of fire.

flowering in *Bulbostylis paradoxa* (Cyperaceae) within just 24 h after the fire. Flowering after fire certainly gives and advantage, since it allows the plant to use available resources without germination barriers and in new and fresh open areas for its establishment [204].

Many structural plant features have been proposed as important tools for fire event survival. Underground roots and stems with carbohydrate, nutrient and water storage have been reported for herbaceous and sub-shrub Neotropical savannah species, allowing them to regrow after the fire has passed [205]. For instance, diffuse underground systems, rhizophores, and xylopodium have been reported for 7 Asteraceae species from the Neotropical savannah [206], which can support the individual life during the dry season and after fire events. Xilopodium, as well as other underground systems, have been found in many species as reported for the *Brosimum gaudichaudii* (Moraceae) shrub [207], the *Ocimum nudicaule* herb (Lamiaceae) [208] and three *Erythroxylum* species (Erythroxylaceae) [209], and may indicate be a convergent trait of many plant species in this environment, often related to species dominance in physiognomies.

Regrowth after fire events requires carbon [79] for the creation of new tissues and organs; however, burning that reaches the leaves reduces the photosynthetic area of the plants [210], consequently decreasing the capture of atmospheric CO_2. The loss of leaf area can be total in herbaceous and shrub plants and partial in some sub-arboreal plants during fire events, whereas tree branches normally are not burnt but are damaged by the hot airflow [79]. In this respect, underground reserve organs may be a fundamental carbon source, mostly consisting of carbohydrates such as starch, fructan, glucose and sucrose [189, 206]. Complex carbohydrates such as starch are hydrolyzed to soluble sugars by hydrolytic enzymes such as the exoamylase β-amylase, which cleaves α-1,4 linkages, and the debranching enzyme isoamylase, which cleaves α-1,6 linkages [211] and the product used for plant development. After leaf regrowth, the new leaves of some plant species may return with higher photosynthetic rates, stomatal conductance and nitrogen concentration than during the pre-burn period [212], with high vigor and potential for growth [213]. However, these responses did not occur in *Vochysia cinnamomea* (Vochysiaceae), a native species of Neotropical savannah, since fire did not exert a direct influence on its physiological processes [214].

The bark structure and thickness of tree plants has been cited for years as one of the greatest protective traits against fire in the Neotropical savannah, preventing damage to the vascular cambium [215] and deformations of the xylem [216] and phloem. The thick corky bark may protect internal stem tissues [217], reducing mortality and maintaining water and solute transport during and after the fire episodes [218]. On this basis, the bark properties have been studied across 31 species from the Neotropical savannah, providing shreds of evidence that the outer bark acts as mechanical support and defense against pathogen attack and the inner bark as a place related to storage and transport of water [218]. Other less frequent and more specific characteristics have also been discussed regarding fire survival. For instance, *Vellozia variabilis* (Velloziaceae) has resin glands on its leaves that produce flammable substances capable of starting quick-burning on the more protected plant base, preventing damage to more sensitive upper plant portions [219]. Due to these plant specificities, as well as abiotic and biotic conditions, the Neotropical savannah is a potential environment for new structural and ecological discoveries.

Finally, the occurrence of invasive tree species in open areas of the Neotropical savannah has altered the microclimate conditions, affecting grasses and shrubs and consequently the dynamics of fire occurrence in the Neotropical savannah [124, 220]. This cascade of events will certainly have a negative impact on the plant and animal communities of the Neotropical savannah, changing the local landscape.

7. Conclusions

In the current chapter, we report the most common types of abiotic stress in Neotropical savannah plant species, which can simultaneously influence and determine the different functional types of plants. Plant species are affected and respond differently to abiotic stress in the Neotropical savannah, mostly in terms of more specific characteristics such as microhabitat, seasonality, topography and anthropic interference. Moreover, Neotropical savannah plant species have evolved over thousands of years subject to various types of abiotic stress (i.e. water seasonality, high temperature and light availability, soil with a deficiency of essential nutrients, and fire). All of them have been shaping differently the Neotropical savannah physiognomies, and recent changes in abiotic conditions are occurring in a very rapid manner, mainly due to anthropogenic actions over the last decades. Reduction of native vegetation areas, expansion of agriculture and extensive pecuary, changes in the fire regime and the introduction of nutrients, such as nitrogen and phosphorus, are examples that have been reported for Neotropical savannah in recent times and that may potentially have negative effects on biodiversity. In view of this reality, conservation strategies for the remaining area should be discussed with society and prioritized in government policies in order to conserve such areas and to encourage the sustainable use of the Savannah wealth.

Author details

Silvana Aparecida Barbosa de Castro[1*] and Vinícius Coelho Kuster[2]

1 Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil

2 Unidade Acadêmica de Ciências Biológicas, Universidade Federal de Jataí, Jataí, Goiás, Brazil

*Address all correspondence to: silvana.abcastro@gmail.com

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